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The N400 as an index of lexical preactivation and its implications for prediction in language comprehension

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ABSTRACT
The N400 component's amplitude is standardly reduced for predictable words. But it is not clear whether this reduction truly reflects preactivation of the critical word or whether it just indexes the difficulty of integrating the word with the sentence. To adjudicate between these two accounts, event-related potentials were recorded while participants read short stories. In half of the stories, just before the story-final sentence, we induced an explicit prediction of a congruent or an incongruent target word, thereby preactivating this word. Inducing prediction for the incongruent target word eliminated the N400, fully supporting the preactivation theory. This implies that the N400 is a marker of prediction and that prediction is an essential aspect of sentence comprehension. In addition, an analysis of the ERPs on the words preceding the critical target word provides evidence on how the target word becomes preactivated by the context.

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1. Introduction

The ubiquity of predictions in language comprehension is a matter of mounting debate. In recent years several findings demonstrate that in specific situations, discourse context information leads to the prediction of a word that will actually only occur in the input later. Prediction here thus refers to the fact that a word´s memory representation becomes activated before this word is actually present in the input. For example, ERP research shows that when a noun (Van Berkum, Brown, Zwitserlood, Kooijman, & Hagoort, 2005; Wicha, Moreno, & Kutas, 2004) or a class of nouns (Szewczyk & Schriefers, 2013) is highly predictable, these nouns are preactivated before the occurrence of the noun. Studies employing the "visual world" paradigm show that listening to a sentence prompts the listeners to look at objects that are likely to be mentioned in the near future (Altmann & Kamide, 1999; Kamide, Altmann, & Haywood, 2003). Such findings led some researchers to propose that predictions are part-and-parcel of language comprehension, a mechanism that helps understanding spoken or written discourse (Dell & Chang, 2014; Pickering & Garrod, 2013), in line with more general theories which assume that prediction is a core mechanism of brain function (e.g. the predictive coding framework; Friston, 2010; Rao & Ballard, 1999).[1] However, other researchers point to the fact that the bulk of research on predictions uses materials that make the target word very highly predictable. This opens the possibility that predictions are just an epiphenomenon of language processing which in very specific situations can support language comprehension, but otherwise do not have consequences for language comprehension (Huettig & Mani, 2016).

One way of resolving this issue is to focus on the N400 event-related potential component. The N400 component is ubiquitous and occurs when processing any conceptually meaningful stimuli. It is elicited by all words (or other meaningful stimuli) and its amplitude reflects the extent to which a word's meaning is congruent with the meaning of the context in which it occurs (for example the preceding part of a sentence). When the word is incongruent, it gives rise to a large N400, and when the word is congruent, the amplitude of the component is reduced. One theory – the preactivation theory – posits that this reduction is a consequence of the fact that the congruent word was predicted on the basis of the preceding context (Kutas & Federmeier, 2000; Kutas & Federmeier, 2011; Lau, Phillips, & Poeppel, 2008; Van Berkum, 2008). According to this theory, the N400 is evoked during so-called lexical access, that is a process during which the representation of a word is activated or constructed in long-term memory. It posits that coherent sentences automatically preactivate words that are congruent with the sentence.

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As a result, when such a word is encountered in the input, it does not elicit the N400 because its representation is already activated to some degree and thus accessing this word is easy. Conversely, when the word is incongruent, it elicits the N400, because its representations have not been preactivated and full lexical access has to be carried out.

However, the finding that incongruent words lead to the N400 component could also be explained by another theory, which does not associate it with prediction. The integration theory proposes that the N400 is an index of incongruity and arises during so-called semantic integration, a hypothesised stage of language comprehension during which the word, after already having been retrieved from long-term memory, is integrated with the conceptual representation of the preceding part of the sentence (Brown & Hagoort, 1993; Hagoort, 2008; Sereno, Rayner, & Posner, 1998). The meaning of a congruent word is easy to integrate with the meaning of the context, whereas the meaning of an incongruent word is difficult to integrate. According to this account, integration is a strictly bottom-up process. It can occur only after the word has appeared as a part of the sentence and lexical access has been initiated. The integration account thus holds that modulations of the N400 component cannot be a consequence of prediction (Hagoort, 2008).

An empirical test contrasting these two accounts could have far-reaching consequences for our understanding of the role of prediction in language comprehension, given the prevalence of the N400 (it is elicited by all words) and its reliability (it is one of the most robust and easiest to observe ERP components). If the preactivation theory is correct, it means that modulations of the N400 component's amplitude are an index of the extent to which a word has been predicted (with prediction understood in the specific sense of lexico-semantic activation). By contrast, if the integration theory is correct, we cannot conclude anything about predictions in a given sentence based on the component's amplitude.

Five classes of findings are relevant for the question which theory better explains the N400 component. The first finding is that the amplitude of the N400 correlates with the cloze probability of the word, an index of the word's predictability (DeLong, Urbach, & Kutas, 2005; Kutas & Hillyard, 1984). Cloze probability of a word corresponds to the proportion of people who would continue a given sentence with the given word. For example, in the sentence "Her dress was made of nice … ", "silk" has a cloze probability of 0.6, while "tar" has a cloze probability < 0.01, because people tend to continue the sentence with "silk", but not with "tar". Words with a high cloze probability elicit N400s with small amplitudes. According to the preactivation theory, this is because words of high cloze probability introduce relatively little new information over and above the preceding context and thus recognition and access to such words is greatly facilitated. In contrast, words with low cloze probability are more surprising, because their semantic properties are not included into the representation of the preceding part of the sentence and thus more time and effort is needed to arrive at a stable conceptual representation of the sentence including the new word, giving rise to an N400. By contrast, integration theory would explain this finding by the fact that cloze probability and congruity of a word in a sentence are strongly correlated, and thus congruent words are easier to integrate with a preceding context than incongruent words.

The second finding relates the N400 to the accruing representation of sentence meaning. Each word in a sentence elicits an N400. Words occurring at the beginning of a sentence elicit large N400s and for a coherent sentence the amplitude of the N400 decreases with each new word (Van Petten & Kutas, 1990). Thus, the richer the representation of the sentence is, the less surprising are coherent continuations. This finding can, of course, also be explained in terms of cloze probability. Since a sentence can start with almost any word, cloze probability of the first word(s) is very low. Once the unfolding sentence starts to set up a semantic context, congruent words start to have a much higher cloze probability than other words. Because word position in coherent sentences correlates with cloze probability, both preactivation and integration theory can account for this finding.

The third piece of evidence comes from a study by Federmeier and Kutas (1999). They showed that a word that is semantically closely associated with the semantically best fitting word in a sentence gives rise to a reduced N400 amplitude, even if this word is – given the preceding context – unexpected. The authors presented participants with short stories ("They wanted to make the hotel look more like a tropical resort. So along the driveway they planted rows of … "), which could be continued either with an expected word ("palms"), a word that was closely related to the congruent word but unexpected ("pines"), or a word that was semantically less related but equally unexpected ("tulips"). Related unexpected words ("pines") had reduced N400 amplitude, relative to the less related unexpected word ("tulip"). Critically, the reduction of the N400 for related words was larger when the word was embedded in highly constraining contexts. This happened despite the fact that more constraining contexts render unexpected words less plausible. This result, however, starts to make sense when one assumes that highly constraining contexts strongly preactivate conceptual features of the congruent words. When an unexpected word is presented, it can still benefit from this preactivation, as long as it is related to the congruent word. In the example above, this is exactly the case with the word "pines", which is related to the expected word "palms". This study thus strongly suggests that semantic features of an expected word become active before this word is actually present in the input. This finding is not easily accounted for by integration theory. Integration theory would predict that all unexpected words will elicit equally large N400s, irrespective of whether they are or are not related to the expected word.

The forth piece of evidence comes from repetition priming. ERP studies have shown that repetition priming leads to a reduced N400 amplitude on a target preceded by an identical prime, relative to the same target not preceded by an identical prime. This effect occurs both when words are repeated in lists of words (Bentin & Peled, 1990; Karayanidis, Andrews, Ward, & McConaghy, 1991; Neville, Kutas, Chesney, & Schmidt, 1986; Olichney et al., 2000; Rugg, 1985, 1990; Rugg & Doyle, 1992; Rugg, Furda, & Lorist, 1988; Van Petten & Senkfor, 1996) and when words are repeated in sentences (Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991). This reduced N400 amplitude is readily explainable as being due to the preactivation of the target by the identical prime. It is much more difficult to explain this effect in terms of the integration theory. A mere repetition of a word should not affect the ease of word's integration with a context, especially when the "context" is nothing else than a list of unrelated words. Since the N400 repetition effect occurs for lags as long as 20 unrelated words (Rugg, 1990), participants would have to integrate blocks of at least these 20 unrelated words to justify interpretation of the N400 repetition effect in terms of semantic integration. Obviously, this seems rather unlikely.

Finally, preactivation theory finds support in artificial neural network models of sentence processing. These models are trained to assign a probability distribution to all words in the lexicon at a given position in the sentence, based on the preceding part of the sentence. It has been found that the N400 correlates with the network's surprise (Frank, Otten, Galli, & Vigliocco, 2015) or the prediction error of the network (Rabovsky & McRae, 2014), both of which measure the divergence between the network's contextual prediction and the actual input. This suggests that the same type of computations can be carried out at the neural level in humans. Finding that the N400 correlates with surprise as based on corpus-based statistical patterns of word co-occurrence (which are oblivious to word meanings) speaks against the integration account (cf. Frank et al., 2015).

The present paper addresses the relation between the N400 and its potential interpretation in terms of preactivation. The above summary shows that the available evidence leans in favour of the preactivation account of the N400. However, the evidence supporting an interpretation of the N400 as preactivation is mostly correlational: the N400 amplitude elicited by a word is related to the cloze probability of the word or to an index of context-based predictability, estimated either based on the serial position of the word in the sentence or based on the prediction error in artificial neural networks. Such findings do not provide a direct test of the preactivation theory. They only show a link between the context-based predictability of a word and the amplitude of the N400, while preactivation theory claims that the context-based predictability determines the activation level of a word and that this activation level drives the N400.

Thus, to date there has been no experimental test of the pre-activation theory of the N400, in particular no test that systematically manipulates the pre-activation level of a word independently of its context-based predictability. In this study we experimentally test one of the central tenets of preactivation theory of the N400, namely that the amplitude of the N400 component does not directly depend on a word's congruity with the context, but rather on the (pre-) activation level of the conceptual representations of the word.

1.1. The present study

We presented participants with short stories, each a few sentences long. The story-final sentence of each story contained a target word, which did either fit semantically into the sentence (the congruent condition) or introduced a semantic incongruity (the incongruent condition). According to preactivation theory, in the congruent condition the activation of the target word builds up as the reader goes through the story. At the time when he or she encounters the target word, its activation should be strong enough to considerably reduce the effort required to recognise and access it, yielding a reduced N400 amplitude. In the incongruent condition the target word is not semantically or associatively related to the story, and does not get activated by the preceding portion of the story. When the target noun is encountered, it is effortful to recognise and access it and a full-blown N400 ensues. Thus, in this simple design, the word's contextual predictability and its activation level are coupled, making it impossible to distinguish which of them the N400 is sensitive to.

To break this coupling between the target word's congruity and its activation level, we introduced an additional manipulation. In half of the items, just before the last sentence of the story, participants were presented with the target word and they were informed that this word was going to appear in the next sentence (see Figure 1). Hereafter, we will refer to this condition as the induced-prediction condition. In the other half of items such predictive information was not given (hereafter the no-induced-prediction condition). Apart from the prediction inducing information, the stories were identical in both conditions. These induced predictions should increase the activation level of the target word without altering the word's congruity or incongruity with the sentence. This manipulation thus allows us to dissociate preactivation and congruity and to test the assumption of preactivation theory that the N400 amplitude is a function of the activation level of the target word and not a function of its congruity. The factors Congruity (congruous vs incongruous target word) and Induced Prediction (induced prediction vs no-induced-prediction) were fully crossed, resulting in four conditions: induced-prediction congruent, induced-prediction incongruent, no-induced-prediction congruent, and no-induced-prediction incongruent.

In the no-induced-prediction congruent and the no-induced-prediction incongruent conditions, no explicit prediction is induced and the stories are identical up to the presentation of the target word – "shark" or "doctor" in the example of Figure 1. Thus, at the target word we expect the standard ERP response to semantic incongruities, i.e. an N400 effect for the no-induced-prediction incongruent ("doctor") relative to the no-induced-prediction congruent condition ("shark"). In the induced-prediction congruent and the induced-prediction incongruent conditions, the prediction of the target word is experimentally induced just before the onset of the story-final sentence. Therefore, the two conditions differ from each other at two points: at the point where the prediction is induced and at the point where the target word is presented as a part of the story-final sentence. The preactivation theory predicts that once the conceptual representation of the target word is activated, the N400 evoked by the target word presented as a part of the story-final sentence should no longer be affected by the target word's congruity with the sentence. Therefore, if the prediction inducing information successfully activates the conceptual representations of the target word (and if this activation is still present when the target word is presented as a part of the story-final sentence), we should observe a diminished, or ideally, obliterated N400 for the target word, independent of whether the word is congruent ("shark") or incongruent ("doctor") with the story. The N400 amplitude at the target word in the induced-prediction congruent and induced-prediction incongruent condition should be equal or lower (i.e. less negative) than the N400 evoked in the no-induced-prediction congruent condition.

To sum up, if the preactivation theory is correct, we expect that in the no-induced-prediction congruent, induced-prediction congruent and induced-prediction incongruent conditions the target word will elicit a reduced N400 component or no N400 component at all, because in all these three conditions the target word´s conceptual representation is already activated by the time the target word is encountered: in the no-induced-prediction congruent condition by the supportive context, in the induced-prediction incongruent condition by the induction of prediction, and in the induced-prediction congruent condition by both. Only in the no-induced-prediction incongruent condition the target word does not get activated prior to its presentation and thus it should elicit a full-blown N400. By contrast, if the integration account is correct, we should observe an N400 in both conditions in which the target word is incongruent (no-induced-prediction incongruent, induced-prediction incongruent), regardless of whether a prediction is induced or not.

In our study, we induce a lexical prediction, that is, participants are made to predict a specific word. This prediction may be different from naturally generated predictions, as natural predictions are not necessarily lexical. They can be conceptual and concern broad semantic categories of words and they can also be syntactic, orthographic, or phonological (see Kuperberg & Jaeger, 2016). Also, once a natural prediction turns out to be wrong, it is likely to be either dropped or adjusted, whereas in our study participants can be sure that the predicted word will eventually appear somewhere in the sentence. Inducing the prediction before the story-final sentence, in a paradigm similar to repetition priming, may seem artificial, but it is a compromise. On the one hand, we want to set up the prediction as close to the critical word as possible, but on the other hand we want to avoid interrupting the story-final sentence. Also, the explicit character of the manipulation might seem unnecessary. However, we want the activation to be as strong as possible and not to fade away too quickly, and less explicit manipulations do not guarantee that we reach this goal. For example, masked semantic priming is known to elicit activation that lasts no longer than several hundreds of milliseconds before it washes away (Greenwald, Draine, & Abrams, 1996). Similarly, the activation of contextually inappropriate meanings of words quickly vanishes (Marslen-Wilson, 1987). In contrast, repetition priming has been shown to produce activations that are longer lasting and which, importantly, also affect the N400

	no-induced-prediction		induced-prediction	
	congruent	incongruent	congruent	incongruent
context sentences	*My uncle loves to make practical jokes. During the last summer he mounted a triangle fin on his back, jumped into the water and approached the swimming area with his fin only above the water.*			
induction of prediction / no information			*In the upcoming sentence you will see the following word: (shark)*	*In the upcoming sentence you will see the following word: (doctor)*
critical story-final sentence	*There was terrible fuss and everybody thought they saw a* ***shark*** *approaching them.*	*There was terrible fuss and everybody thought they saw a* ***doctor*** *approaching them.*	*There was terrible fuss and everybody thought they saw a* ***shark*** *approaching them.*	*There was terrible fuss and everybody thought they saw a* ***doctor*** *approaching them.*

Figure 1. Example of an experimental item in the four experimental conditions.

component (Bentin & Peled, 1990; Besson & Kutas, 1993; Besson, Kutas, & Van Petten, 1992; Karayanidis et al., 1991; Mitchell, Andrews, & Ward, 1993; Neville et al., 1986; Olichney et al., 2000; Rugg, 1985, 1990; Rugg et al., 1988; Rugg & Doyle, 1992; Van Petten et al., 1991; Van Petten & Senkfor, 1996). It has been shown that at least in an interval of 5 min or 20 items between the prime and the target the effect of repetition on the N400 component is preserved, although it is not as strong, as when the target is immediately repeated (Kim, Kim, & Kwon, 2001; Nagy & Rugg, 1989; Rugg, Mark, Gilchrist, & Roberts, 1997; Van Petten et al., 1991). We expect that making participants strategically expect the word will further ensure that its conceptual representation will be active at the time when the target word is encountered. If the preactivation theory is correct, it should not matter how exactly the word's representations have been activated.

Apart from addressing the question of the cognitive mechanism underlying the N400 component, the induced prediction manipulation also opens the possibility to test the ERP correlates of processing a sentence while holding an explicit word prediction. This question concerns the words following the prediction induction point, but preceding the target word (in the above example, "There was terrible fuss and everybody thought they saw"; we will refer to them as intervening words). Until now, ERP research on lexical predictions in language comprehension focussed on testing if the word is predicted at a directly preceding element (e.g. prediction of a noun tested at a prenominal adjective: Van Berkum et al., 2005; Wicha et al., 2004). These studies showed that when a word is strongly supported by the context, it is activated already at a directly preceding word. These studies do not show, however, how, once a prediction is made, it is carried to the point where the predicted word is encountered, and whether it has any consequences for the processing the intervening words. This is exactly the type of questions we can look into by comparing the ERPs evoked by the intervening words in the induced-prediction congruent, induced-prediction incongruent, no-induced-prediction congruent and no-induced-prediction incongruent conditions.

There are several possibilities for how a specific lexical prediction can affect processing of the intervening words. The first possibility is that predictions affect sentence processing from the very point they are made. In this scenario, the (induced) predicted word will be related to the conceptual representation of the discourse (i.e. the part of the story presented until this point) right from the point of prediction induction onwards.

Another possibility is that predictions act locally and they come into play only at the point where they are relevant for sentence processing. In this scenario, the (induced) predicted word will not be integrated with the conceptual representation of the story. Instead, the predicted word will be stored in working memory as participants read through the story-final sentence. Only at a point where the predicted word becomes relevant and has a high chance to occur soon, the predicted word will be retrieved from working memory and its conceptual representation will become (re)activated. It should be kept in mind that these analyses are exploratory and we do not have any specific hypotheses concerning the ERPs at the intervening words. In the general discussion we will show how the ERP results at the intervening words relate to these two scenarios.

2. Materials and methods

2.1. Participants

We recruited 36 right-handed native speakers of Polish (26 women and 8 men, mean age 21 years, and range

18–28 years) from the subject pool of the Institute of Psychology at the Jagiellonian University in Cracow, Poland. None had experienced neurologic trauma or had any neurologic impairment.

2.2. Materials

160 short stories, consisting of 2–6 sentences, were constructed. The final sentence of each story contained a transitive verb, followed by a direct object noun (the target word), and at least one additional word. The story-final sentences had SVO structure – the canonical word order for Polish. In order to prevent participants from strategically adapting to a constant number of intervening words (i.e. words that follow the prediction induction point, but precede the occurrence of the target word itself) and to a fixed position of the target noun in the story-final sentence, we varied the number of the intervening words (mean 5.6, range 2–11, SD 2.26).

In a paper-and-pencil cloze test, each story was truncated in the story-final sentence just before the target word and was shown to at least 15 participants, who were asked to complete the story with the first word(s) that came to their mind. In all stories, the target word was among the two best completions proposed by the cloze test participants. The average cloze score for the target nouns was 0.54, range 0.06–1.00[2], SD 0.27.

From each of the resulting 160 congruent items, an incongruent item was derived. These incongruent items contained a direct-object noun in the story-final sentence that was incongruent with the preceding part of the story. These semantic incongruities were introduced by reassigning target nouns from a given story to the position of the target noun in a different story. The cloze test and inspection by the experimenter confirmed that the new combination of story and target noun resulted in a semantic violation. Up to the target word, the story final sentences were identical across the congruent and incongruent conditions. Appendix A gives examples of stories and story-final sentences in the congruent and incongruent conditions.

Each item was prepared in two versions: induced-prediction and no-induced-prediction (for details, see Procedure), constituting the Prediction factor. This construction of the materials resulted in an experimental design with 2 crossed factors: Congruity (context and target noun are semantically congruent versus incongruent) and Prediction (the reader knows the target word prior to the presentation of the story final sentence or not). The resulting 640 items were divided into 4 experimental lists of 160 items. Each list included 40 items from each of the 4 cells resulting from crossing the Congruity and Prediction factors. Each context story and each target word was used in a list only once.

In order to make the stories more natural to read, we increased the proportion of congruent items by adding 40 congruent filler items to each list. The filler items had the same structure as the experimental items; 20 of these filler items had the prediction inducing information presented just before the story-final sentence, while in the other 20 items no such information was given. The critical and filler items were presented in a randomised order.

2.3. Procedure

Participants were seated in a dimly-lit, sound-attenuated room. Stimuli were presented on a 17″ CRT screen, in white letters on a dark-grey background. Participants were seated approximately 70 cm from the screen. Each item was presented in two parts (see Figure 2). The first part was presented all-at-once, and consisted of all sentences of the story, except the final sentence. These sentences remained on the screen until the participant pressed the spacebar key, indicating that s/he had finished reading the sentences. After the spacebar press, the screen went blank for 1300 ms. After the blank period, in the induced-prediction congruent and induced-prediction incongruent conditions participants saw the following information: "In the upcoming sentence you will see the following word:", with the target word of the story final sentence displayed in the next line. The target word was presented in the same grammatical form as it appeared in the story final sentence (i.e. in accusative case). The target word was displayed in brackets, using a font that was 50% larger than the font used for displaying the story. This presentation mode of the target word was chosen in order to clearly distinguish the prediction-inducing information from the story. The information was displayed for 2 s, followed by 1 s of blank screen. From this moment on, the presentation sequence for the induced-prediction and no-induced-prediction conditions were the same. After the blank period preceding the first word of the story final sentence, a fixation marker ("+++") was presented in the centre of the screen for 500 ms, followed by a 500 ms blank, and by the word-by-word presentation of the final sentence. Each word was displayed for 300 ms, centred in the middle of the screen, followed by a 200 ms blank interval. Prepositions were displayed in the same frame as the word following them; similarly, reflexive verbs were displayed together with the reflexive pronoun ("się"). The main verb and the target noun were always displayed without any accompanying words. 1500 ms after the offset of the last word of the final

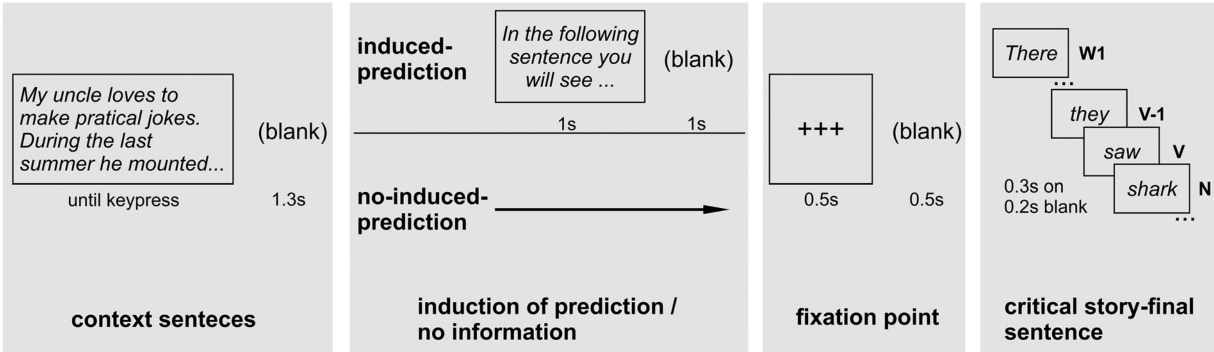

Figure 2. Structure of an individual trial. Abbreviations: W1 – first word of the story final sentence; V-1 – word directly preceding the main verb; V – main verb; N – target noun.

sentence, presentation of the lead-in sentences of the next trial started.

The number of displayed frames (words or pairs of words displayed together) between the onset of the story final sentence and the target noun varied across items (mean: 4.8, range 2–10, SD: 1.9). Merging some content words with adjacent function words was meant to ease reading by avoiding presentation of very short function words alone. In the remaining part of this paper, we will refer to all display frames as "words".

Participants were instructed to read all items carefully, to remain still, and to avoid eye-movements and blinks in the period between the presentation of the prediction-inducing information and the end of the story final sentence. They were also told that, after the experiment, they would have to perform a sentence recognition test. The test was introduced to ensure that the participants maintained their attention while reading the stories. The recognition test consisted of 30 sentences; 10 sentences were identical to the story final sentences of the actually presented items, 10 were similar (a story final sentence with an opposite Congruity value), and 10 completely new. Participants were asked to assign the sentences to one of these three categories (identical, similar, or new). The 20 items from which the identical and similar sentences were taken were equally distributed among the 4 experimental conditions.

The experiment started with a short training session consisting of 6 items. After each block of 50 items, participants were offered a break. The complete experiment (including electrode placement and removal and the off-line recognition test) lasted approximately 2 h.

2.4. EEG recording

EEG was recorded from 32 scalp sites by means of AgAgCl active electrodes (BioSemi Active-Two system) mounted in an elastic electrode cap (Electrocap International) at standard 10–20 system locations. Recordings were referenced to the C1 electrode and re-referenced off-line to the mean of the left and right mastoids. The vertical EOG was monitored with two electrodes placed below and above a participant's right eye, and horizontal EOG was recorded from electrodes at the outer canthi of the eyes. The recordings were digitised online at 256 Hz. EEG was filtered off-line with a high-pass filter (0.2 Hz), to exclude slow-signal drifts.

Epochs from the continuous EEG in the interval between 0 and 900 ms with respect to the onset of the words of interest were averaged and analysed. We analysed the EEG without performing any baseline corrections. A valid baseline would have to be based on the time-window preceding the point in which the procedure for the induced-prediction and no-induced-prediction conditions diverged. However, in many items and participants, this time-window contained movement-related artifacts. Furthermore, many words which we analysed occurred long after this potential baseline time-window (for example, in more than half of the items, the critical noun in the induced-prediction conditions would be separated from the baseline time-window by 7 seconds or more). As a consequence, any artifact occurring in this long time-period would require to remove the whole item from the analysis, which would have led to a massive data-loss (for other studies using similar baseline-free analyses, see e.g. Choudhary, Schlesewsky, Roehm, & Bornkessel-Schlesewsky, 2009; Wolff, Schlesewsky, Hirotani, & Bornkessel-Schlesewsky, 2008).[3]

Systematic artifacts resulting from eye-movements, blinks and motor artifacts were filtered out using a procedure based on ICA (Delorme, Sejnowski, & Makeig, 2007; Jung et al., 2000). Segments containing non-stationary artifacts (such as skin potentials, or artifacts resulting from head-movements) were manually rejected. On average 5% of trials was rejected. They were equally distributed across the experimental conditions.

Six participants were excluded from further analysis because of excessive alpha activity or poor EEG recording quality; another two subjects were excluded due to very poor results in the recognition test (14 and 12 errors in 30 items). This left twenty-eight participants for the final analysis.

3. Results

3.1. Performance on the recognition test

On average, participants correctly classified 22.5 of the 30 sentences presented in the recognition test (range: 17–29, SD: 3.7), indicating that they read the items attentively.

We also tested whether the correct classification of the identical and similar sentences depended on the experimental condition in which these items were seen. To this end, for each participant and each of the four experimental conditions we computed a separate recognition score, based on the number of correctly classified sentences (the maximum possible score was 5). We entered these recognition scores into a repeated-measures ANOVA with Prediction and Congruity as factors. This analysis yielded a significant main effect of Congruity [$F(1, 27) = 7.88$, $p < 0.01$]. Test sentences derived from items in the congruent condition more often were classified correctly than test sentences derived from items in the incongruent condition (mean scores 3.84 and 3.4, for congruent and incongruent conditions, respectively). There was no effect of Prediction and no interaction of Prediction and Congruity.

3.2. Analysis of ERP data

We measured ERPs to the target noun and to the intervening words. An initial analysis showed that the effects of Congruity and Prediction on the intervening words varied with respect to the words' serial position in the story-final sentence. Therefore, in all our analyses, we take into account the intervening word's position in the sentence. However, since the number of intervening words was not constant across items (in order to avoid strategies; for details see Materials), it was impossible to compute continuous ERP waveforms covering all intervening words, across all items. In order to capture the effects of our manipulations at comparable positions across items with varying number of intervening words, we selected three critical positions: the first word of the story-final sentence, the main verb (in all but three items the main verb directly preceded the target word), and the word directly preceding the main verb. However, in 20 items (12.5%) the story-final sentences had only two intervening words. Since the same data from these items would contribute to the analysis on the first word and on the word directly preceding the verb, we excluded these items from the analyses at the word directly preceding the verb.

At the target word we analysed ERPs in 2 time-windows: the 300–500 ms time-window (the time-window of N400 effects), and 500–700 ms (the time window of late positivities). The analysis at the intervening words is more exploratory and thus the time-window of analysis at these words was selected based on visual inspection of the waveforms. Because a modulation with a similar time-course was present at each of the three intervening words positions, starting at around 350 ms and lasting until 700 ms, we chose the same time-window of analysis – 350–700 ms – for the three word position. In the Supplementary Materials S1 we present an additional analysis on all time-points and all electrodes. It largely confirms our selection of the time-window of analysis (with the exception that on the word preceding the main verb there are no significant false discovery rate corrected effects). In order to assess the topographic distribution of experimental effects, we added two topographical variables to the analyses: Anteriority (with 3 levels: anterior, central and posterior) and Hemisphere (with 2 levels: left and right). The two variables delineated the scalp into 6 electrode clusters, each consisting of 4 electrodes. Figure 3 shows the assignment of electrodes to the electrode clusters. These analyses were conducted using multivariate analyses of variance (MANOVA), with

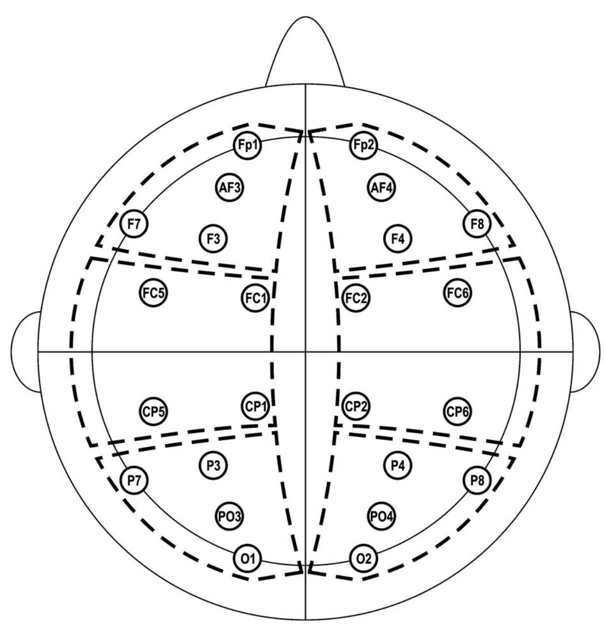

Figure 3. Position of electrodes entering statistical analyses: 24 electrodes divided into six clusters.

Table 1. F- and *p*-values of MANOVAs for words at the three intervening word positions and the target noun in the story-final sentence. Significant effects are bolded.

		First word		Main verb – 1		Main verb		Target noun			
		350–700		350–700		350–700		300–500		500–700	
	Df	F	p	F	p	F	p	F	p	F	p
Prediction (P)	(1, 27)	**22.86**	**<.0001**	**9.75**	**<.01**	**8.85**	**<.01**	**76.29**	**<.0001**	**10.80**	**<.01**
Congruity (C)	(1, 27)	0.02	0.89	2.11	0.16	**27.11**	**<.0001**	**21.52**	**<.0001**	3.07	0.09
Ant.-Posterior (AP)	(2, 26)	**12.16**	**<.001**	**12.67**	**<.001**	**50.09**	**<.0001**	**6.00**	**<.01**	**13.63**	**<.0001**
Hemisphere (H)	(1, 27)	2.01	0.17	**20.46**	**<.001**	**35.13**	**<.0001**	**6.21**	**<.05**	**5.29**	**<.05**
P * C	(1, 27)	2.75	0.11	1.33	0.26	**36.79**	**<.0001**	**35.86**	**<.0001**	**31.69**	**<.0001**
P * AP	(2, 26)	**6.36**	**<.01**	**9.70**	**<.001**	**6.45**	**<.01**	**39.73**	**<.0001**	**16.30**	**<.0001**
C * AP	(2, 26)	0.06	0.95	0.83	0.45	**6.18**	**<.01**	**32.71**	**<.0001**	**4.73**	**<.05**
P * H	(1, 27)	0.01	0.92	0.03	0.87	0.48	0.5	**4.57**	**<.05**	**17.79**	**<.001**
C * H	(1, 27)	3.35	0.08	**5.62**	**<.05**	2.51	0.12	0.06	0.81	**11.12**	**<.01**
AP * H	(2, 26)	0.43	0.65	3.04	0.06	**5.58**	**<.01**	1.27	0.3	3.02	0.07
P * C * AP	(2, 26)	0.28	0.76	0.29	0.75	**4.99**	**<.05**	**19.71**	**<.0001**	**22.80**	**<.0001**
P * C * H	(1, 27)	0.31	0.58	0.70	0.41	**6.47**	**<.05**	0.33	0.57	0.93	0.34
P * AP * H	(2, 26)	2.48	0.1	0.16	0.86	0.21	0.81	1.74	0.2	2.46	0.11
C * AP * H	(2, 26)	0.15	0.86	1.35	0.28	0.57	0.57	0.41	0.67	0.34	0.71
P * C * AP * H	(2, 26)	1.11	0.35	0.12	0.88	1.70	0.2	0.04	0.96	1.31	0.29

the factors: Prediction, Congruity, Anteriority and Hemisphere. Table 1 gives statistical values of all effects for the three intervening word positions (first word, word preceding the main verb, and main verb) and for the two time windows at the target noun. For the sake of brevity, in describing the results, we refer only to effects involving the factors Prediction and/or Congruity.

Most of the abovementioned analyses are exploratory: We did not have any hypotheses, defined at the level of specific ERP components, for the effects at the intervening words, as well as for the late positivities at the target word. Our main focus is on the N400 component at the target noun, because this is the crucial position which should adjudicate between the preactivation and the integration view. For this component we perform additional planned comparisons on amplitudes averaged in the 300–500 ms time-window, across central and posterior electrode clusters, where the N400 typically occurs.

3.2.1. First word of the story-final sentence

Figure 4a shows ERPs from a representative set of electrodes for the first word of the story-final sentence. Throughout the whole epoch, the ERPs for the no-induced-prediction congruent and no-induced-prediction incongruent conditions stayed on top of each other. At the very beginning of the epoch, the ERPs for the induced-prediction congruent and induced-prediction incongruent conditions showed a centro-parietal positivity, relative to the no-induced-prediction congruent and no-induced-prediction incongruent conditions. This effect seems to be a spill-over from the period between the prediction induction point (in the induced-prediction condition) and the onset of the story-final sentence. This positivity disappeared before 400 ms.

In the 280–700 ms latency range, the ERP waveforms for the induced-prediction conditions (induced-prediction congruent and induced-prediction incongruent) gave rise to an antero-central negativity, relative to the no-induced-prediction conditions (no-induced-prediction congruent and no-induced-prediction incongruent). In a late part of this time-window, the negativity for the induced-prediction incongruent condition was more pronounced, than in the induced-prediction congruent condition. Statistical analysis in the 350–700 ms time-window revealed a significant main effect of Prediction, and an interaction of Prediction and Anterior-Posterior. Follow up contrasts showed that the Prediction effect most significant the anterior and central electrode clusters (1.26 µV, $p < .0001$; 1.21 µV, $p < .0001$; and 0.61 µV, $p < .05$ for anterior, central and posterior electrode clusters, respectively).

3.2.2. Word directly preceding the main verb of the story-final sentence

Figure 4b shows the ERPs evoked by the word directly preceding the main verb, broken down by Prediction and Congruity. The epoch started with a centrally-distributed negativity for the induced-prediction congruent and induced-prediction incongruent conditions, relative to the no-induced-prediction congruent and no-induced-prediction incongruent conditions, that lasted until 150 ms. This negativity was probably a spill-over of an effect of Induced Prediction occurring at a previous (not analysed) word. At around 380 ms a negativity reappeared and it lasted until 600 ms for the induced-prediction congruent condition, and 700 ms for the induced-prediction incongruent condition. The negativity had a central distribution, and was slightly more pronounced for the induced-prediction incongruent condition, especially in its later part. The MANOVA for the 350–700 ms time-window showed a main effect of Prediction and an interaction of Prediction and Anterior-Posterior.

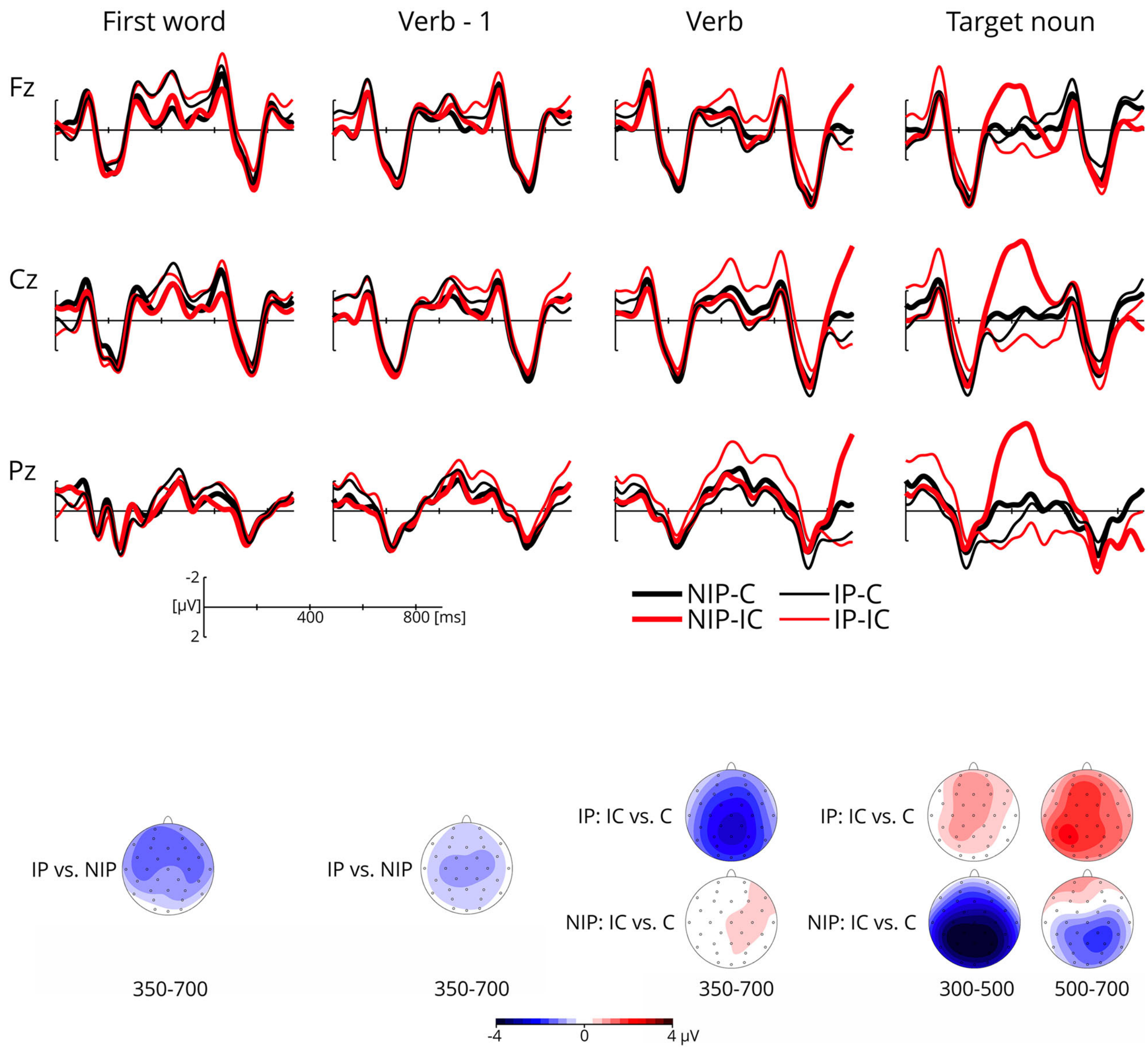

Figure 4. Upper panel: ERPs to the three intervening words: a) the first word, b) word preceding the main verb, c) the main verb, and d) the target noun. ERPs are broken down by Prediction and Congruity (no-induced-prediction congruent (NIP-C) – bold black, no-induced-prediction incongruent (NIP-IC) – bold red, induced-prediction congruent (IP-C) – thin black, induced-prediction incongruent (IP-IC) – thin red). The plots for the word preceding the main verb is based on 140 items, while the remaining plots are based on 160 items. ERPs were filtered using a 12 Hz low-pass filter for visualisation only. Lower panel: voltage maps displaying differences between selected conditions.

Resolving the interaction by Anterior-Posterior confirmed the central distribution of the Prediction effect (0.47 µV, $p < .05$; 7.7 µV, $p < .001$; and 4.6 µV, $p < .05$ for anterior, central, and posterior electrode clusters, respectively). There was also an interaction of Congruity and Hemisphere. Follow-up *t*-tests showed that ERPs for the incongruent conditions (no-induced-prediction incongruent and induced-prediction incongruent) are more negative than ERPs for the congruent conditions (no-induced-prediction congruent and induced-prediction congruent) at the left hemisphere (0.35 µV, $p < .05$), but not at the right hemisphere (n.s.).

3.2.3. The main verb of the story-final sentence

The epoch for the main verb started with a spill-over effect from the preceding word: a negativity for the induced-prediction incongruent and induced-prediction congruent conditions which lasted until 200 ms (see Figure 4c). After 300 ms, the ERP waveforms for the induced-prediction conditions diverged: the induced-prediction incongruent condition led to a centro-parietal negativity, while the induced-prediction congruent condition elicited a centro-parietal positivity, relative to the no-induced-prediction conditions (no-induced-prediction congruent and no-induced-prediction incongruent).

Statistical analysis in the 350–700 ms latency range revealed main effects of Congruity and Prediction, and an interaction of Congruity and Prediction that was further qualified by three interactions with Anterior-Posterior: an interaction of Prediction and Anterior-Posterior, an interaction of Congruity and Anterior-Posterior, and an interaction of Prediction, Congruity and Anterior-Posterior. Resolving the highest-level interaction confirmed that waveforms for the two no-induced-prediction conditions (no-induced-prediction congruent vs. no-induced-prediction incongruent) did not differ from each other at any level of the Anterior-Posterior factor (ps > .29). They also revealed that induced-prediction incongruent was more negative than no-induced-prediction incongruent, particularly at central and posterior electrodes (frontal: 1.04 µV, $p < .001$; central: 1.67 µV, $p < .0001$; posterior: 1.43 µV, $p < .0001$), whereas induced-prediction congruent was significantly more positive than no-induced-prediction congruent at central and posterior electrodes (frontal: n.s., central: 0.49 µV, $p < .05$; posterior: 0.74 µV, $p < .01$). The effects of Prediction and Congruity were also modified by an interaction of Prediction, Congruity and Hemisphere. This interaction was primarily driven by the induced-prediction congruent being more positive than induced-prediction incongruent over the right (0.67 µV, $p < .01$), but not the left hemisphere (n.s.).

Summing up, in contrast to the preceding words, the presentation of the main verb drove waveforms for the induced-prediction congruent and induced-prediction incongruent conditions in opposing directions: the induced-prediction incongruent condition led to a centro-parietal negativity, while the induced-prediction congruent condition led to a centro-parietal positivity (more right-lateralized), relative to the no-induced-prediction conditions (no-induced-prediction congruent, no-induced-prediction incongruent).

3.2.4. The target noun

As can be seen in Figure 4d, at the target noun the data patterned in a radically different way than at the verb. First we will focus on the effect of Congruity in the no-induced-prediction conditions. Throughout all intervening words the ERP waveforms from the no-induced-prediction congruent and no-induced-prediction incongruent conditions remained on top of each other. This pattern changed 200 ms after the presentation of the target noun, when the ERP in the no-induced-prediction incongruent condition showed a centro-parietal negativity relative to the no-induced-prediction congruent condition, reflecting the standard N400 effect to semantic incongruities, at 680 ms changing into a posteriorly distributed positivity (a P600 effect), which remained until the end of the recorded epoch.

In the induced-prediction conditions (induced-prediction congruent and no-induced-prediction incongruent), the Congruity manipulation had a clearly different effect. The ERP waveform in the induced-prediction congruent condition started with a centro-parietal positivity, relative to the no-induced-prediction congruent condition (a spill-over from the preceding word). The positivity continued until 450 ms, reaching its maximum in the 300–400 ms latency range. After 450 ms the waveforms for induced-prediction congruent and no-induced-prediction congruent conditions aligned, except for left-central electrodes, where in the 450–750 ms time-window the induced-prediction congruent condition led to a weak left-central negativity, relative to the no-induced-prediction congruent condition. The ERP evoked in the induced-prediction incongruent condition also began with a spill-over effect from the previous word – a centro-parietally distributed negativity (relative to the no-induced-prediction congruent condition) that lasted until 250 ms after the target noun onset. After 300 ms, the induced-prediction incongruent waveform gave rise to a widely distributed positivity, both at anterior (an Anterior Positivity) and posterior loci (LPC/P600 effect). The ERPs for the induced-prediction incongruent and no-induced-prediction incongruent conditions aligned at 550 ms at the anterior electrodes and at 700 ms at the posterior electrodes.

The statistical analysis in the 300–500 ms time-window showed main effects of Congruity and Prediction, and a significant interaction of Congruity and Prediction. These effects were further qualified by three interactions with Anterior-Posterior: an interaction of Prediction and Anterior-Posterior, an interaction of Congruity and Anterior-Posterior, and a 3-way interaction of Prediction, Congruity and Anterior-Posterior. Follow-up analyses revealed that the Congruity by Prediction interaction was significant at all three levels of Anterior-Posterior, but strongest at centro-parietal electrodes, anterior: $F(1, 27) = 18.07$, $p < .001$, central: $F(1, 27) = 39.46$, $p < .0001$, posterior: $F(1, 27) = 29.57$, $p < .0001$. *t*-tests confirmed the centro-parietal distribution of the N400 effect between the no-induced-prediction congruent and no-induced-prediction incongruent conditions (anterior: 1.04 µV, $p < .001$; central: 2.92 µV, $p < .0001$; posterior: 3.29 µV, $p < .0001$). In addition, the induced-prediction congruent condition led to a centro-parietal positivity, relative to the no-induced-prediction congruent condition (anterior: n.s.; central: 0.55 µV, $p < .05$; posterior: 1.03 µV, $p < .001$). Finally, the induced-prediction incongruent condition was more positive than the induced-prediction congruent condition, but only at the anterior electrode clusters (anterior: 0.77 μV, $p < .01$; central and posterior: n.s.), reflecting an Anterior Positivity effect. Because in the 300–500 ms time-window we were particularly interested in testing if Prediction and Congruity interactively modulate the N400 component, we also conducted planned comparisons on averaged amplitudes in central and posterior electrode clusters (where the N400 is known to have a maximum amplitude). These analyses confirmed that while for the no-induced-prediction condition there is a substantial effect of Congruity, $t(27) = 9.05$, $p < .0001$, for the induced prediction condition there is no such effect, $t(27) = -1.44$, $p = .16$ (see Figure 5). Moreover, both induced-prediction conditions led to more positive N400s, relative to the no-induced-prediction congruent condition (induced-prediction congruent: $t(27) = -3.5$, $p < .01$; induced-prediction incongruent: $t(27) = -3.44$, $p < .01$).

Analysis in the 500–700 ms latency range revealed a main effect of Prediction, which was further qualified by three interactions: an interaction with Congruity, an interaction with Anterior-Posterior, and by a 3-way interaction with Congruity and Anterior-Posterior. The interaction of Prediction and Congruity was significant at the central and posterior electrode clusters ($F = 39.10$, $p < .0001$, and $F = 36.74$, $p < .0001$, respectively) and marginally significant at the anterior electrode clusters ($p = .09$). Additional t-tests showed that in the 500–700 ms time-window the no-induced-prediction incongruent condition was still more negative than the no-induced-prediction congruent condition (a late part of the N400 effect; significant only at the central: 0.85 μV, $p < .05$, posterior: 1.12 μV, $p < .01$, but not at the anterior electrode cluster). They also showed that the induced-prediction congruent condition was significantly different from the no-induced-prediction congruent condition only at the central electrode cluster (0.57 μV, $p < 0.05$), reflecting the negativity at the left-central electrodes for the induced-prediction congruent condition relative to the no-induced-prediction congruent condition. Finally, the t-tests confirmed that the induced-prediction incongruent condition remained more positive than the three remaining conditions in the 500–700 ms time-window (when tested against induced-prediction congruent, anterior: 1.17 μV, $p < .01$; central: 1.55 μV, $p < .001$; posterior: 1.62 μV, $p < .001$). This positivity reflects an Anterior Positivity at the frontal electrodes, and a P600/LPC effect at the parietal electrodes. There were also two significant interactions of Congruity and Prediction with Hemisphere. These interactions were caused by the scalp distribution of the late part of the N400 effect for the no-induced-prediction incongruent waveforms that was shifted to the right: overall, the no-induced-prediction conditions (no-induced-prediction congruent and no-induced-prediction incongruent) and the incongruent conditions (no-induced-prediction incongruent and induced-prediction incongruent) were more negative over the right, relative to the left hemisphere ($ps < .01$), with no difference between the hemispheres for the induced-prediction conditions (induced-prediction congruent and induced-prediction incongruent; $p = .98$) and for the congruent conditions (no-induced-prediction congruent and induced-prediction congruent; $p = .78$).

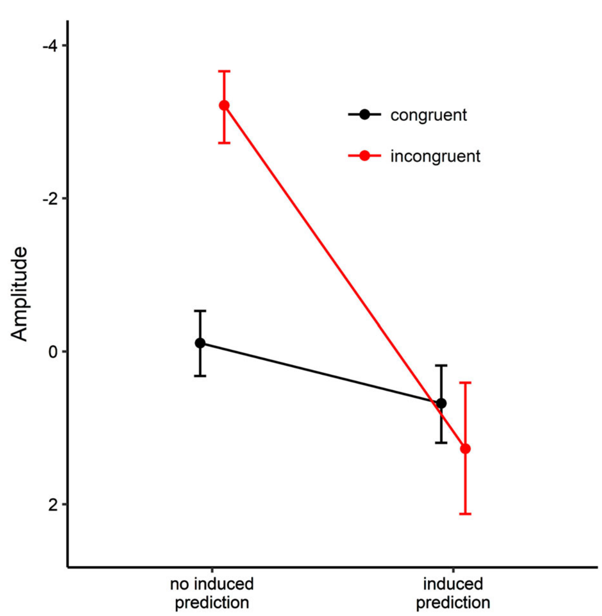

Figure 5. Mean N400 amplitude in the 300–500 ms time-window on central and posterior electrode clusters. Error bars represent 95% confidence intervals.

4. Discussion

In this study, we focussed on the mechanisms underlying the N400 component to find out whether all modulations of the component can be understood as reflecting predictive processing. We dissociated two possible sources of the N400: absence versus presence of lexical preactivation of a target word, or ease of integration, i.e. congruity versus incongruity of the target word with the preceding context. We did so by inducing an explicit prediction of the target word, just before the sentence containing this target word, while manipulating the target word's congruity with the sentence. Preactivation theory assumes that the critical target word should yield an N400 only in the no-induced prediction incongruent condition because only in this condition the target word will not be preactivated. In contrast, integration theory posits that all conditions containing an incongruity (no-induced-prediction incongruent and induced-prediction incongruent) should yield an N400 effect at the target word. In addition, because the prediction was induced before the sentence containing this word, we could also check how processing of the sentence is affected by holding the explicit prediction of a word.

4.1. ERPs at the target word – what drives the N400 component?

The results clearly show that the N400 occurs only in one condition – no-induced-prediction incongruent – while in the remaining three conditions there is no N400. This result is fully compatible with the preactivation theory, according to which an N400 is obtained when the representation of the word at hand has not been pre-activated. In the no-induced-prediction congruent condition, the target word's representation was activated in the course of processing the preceding congruent sentence. In the induced-prediction incongruent condition, the representation of the target word was activated by inducing the explicit prediction for this word. In the induced-prediction congruent condition, the target word's representation was active for both of the above-mentioned reasons. The only condition in which the representation of the target word was not preactivated is the no-induced-prediction incongruent condition. And this was the only condition leading to a large N400 component. In other words, inducing a prediction for a word suppressed the standard N400 effect occurring when the word is incongruent. These results refute the alternative hypothesis, according to which the N400 depends on the congruity of the word with the context. In typical situations (i.e. no induced predictions), congruity and the word's (potential) preactivation go hand in hand, that is, the more the word is congruent with the context, the more it is (potentially) preactivated. In this experiment we dissociated the two factors to demonstrate that (in)congruity with the context per se does not affect the N400. This confirms that the modulation of the N400 at the target noun was entirely a consequence of preactivation that took place before processing the target word, yielding a strong experimental support for the preactivation theory.

The waveforms following induced prediction (induced-prediction congruent and induced-prediction incongruent) had an even less negative N400 amplitude than the waveform in the no-induced-prediction congruent condition. This completely reduced amplitude of the N400 in the induced-prediction conditions (induced-prediction congruent and induced-prediction incongruent) reflects the fact that target words in the induced-prediction conditions were perfectly predictable (cloze probability, CP = 100%). In contrast, in the no-induced-prediction congruent condition, target words have an average CP of only 54%. When we restricted the analysis in the no-induced-prediction congruent condition to a subset of target words with CP equal to 100%, the N400s elicited by these words were as small as in the induced-prediction congruent and induced-prediction incongruent conditions (see Supplementary Materials S2).

Besides the modulations within the N400 time-window, there were also other ERP effects at the target word. The positivity in the induced-prediction congruent and induced-prediction incongruent conditions extends beyond the N400 time-window, particularly in the induced-prediction incongruent condition. We propose that this positivity reflects the participants' conscious recognition of the previously presented target word. From this perspective, this positivity is similar to the episodic old/new effect that is obtained when participants encounter repeated words in lists of unrelated items (Neville et al., 1986; Olichney et al., 2000; Rugg, 1985, 1990; Rugg et al., 1988; Rugg & Doyle, 1992; Van Petten & Senkfor, 1996). The extended positivity in the induced-prediction incongruent condition may in addition contain the P600 component, reflecting attention attracted by the incongruity (Sassenhagen, Schlesewsky, & Bornkessel-Schlesewsky, 2014; van de Meerendonk, Indefrey, Chwilla, & Kolk, 2011) and/or repair processes (Friederici, Hahne, & Mecklinger, 1996; Hahne & Friederici, 1999; Kuperberg, 2007; O'Rourke & Van Petten, 2011; van Herten, Chwilla, & Kolk, 2006). An analogous P600 effect occurs also when no prediction is induced (no-induced-prediction congruent vs. no-induced-prediction incongruent), although with a later onset, presumably because of the overlap with the N400 component (see Kuperberg, 2007; Sassenhagen et al., 2014; Szewczyk & Schriefers, 2011 for a review of studies showing P600s to pure semantic incongruities in sentence processing).

Finally, the incongruent conditions (no-induced-prediction incongruent and induced-prediction incongruent) led to an Anterior Positivity (also referred to as anterior Post-N400-Positivity, Van Petten & Luka, 2012), relative to no-induced-prediction congruent and induced-prediction congruent conditions. Such effects have been associated with the consequences of a failed prediction, that is, a situation when a strongly constraining context induces participants to predict one word, but a different, plausible but less predictable word appears instead (Brothers, Swaab, & Traxler, 2015; DeLong, Quante, & Kutas, 2014; Federmeier, Wlotko, De Ochoa-Dewald, & Kutas, 2007; Van Petten & Luka, 2012). It has been proposed that in such situations the Anterior Positivity corresponds to the disengagement or inhibition of the previous prediction (Federmeier et al., 2007; Kutas, 1993), suppression of a more dominant word meaning in search of a more contextually appropriate subordinate meaning (DeLong et al., 2014), episodic retrieval of preceding words to reinterpret their meaning (Van Petten & Luka, 2012) and revision of the situation model such that it can accommodate the actually presented word (Brothers et al., 2015; Kuperberg & Jaeger, 2016).

Two observations from the present study may contribute to our understanding of the component. First, previous studies showed that the component is elicited only in high-constraint contexts (Federmeier et al., 2007; DeLong, 2009, Experiment 3b; Wlotko, Federmeier, & Kutas, 2012) and only when the target word is plausible in its context (DeLong et al., 2014). In contrast to these reports, post-hoc analyses showed that the Anterior Positivity in our study was triggered even in stories with a low-constraint context (i.e. both in the induced-prediction incongruent and in the no-induced-prediction incongruent conditions, see Supplementary Materials). Moreover, all our incongruent target words were implausible (and often anomalous) in the context of the preceding story. Thus, our study shows that the component can get evoked in a low-constraint context and by an implausible word. The second observation concerns an independence of Anterior Positivities from conscious expectations, from activation of the word, and from the N400 component, as evidenced by the Anterior Positivity elicited in the induced-prediction incongruent condition. This finding suggests that whatever the predictive mechanism leading to the Anterior Positivity is, it is independent of the N400 and of the level of the target word's activation (see Brothers et al., 2015 for a similar argument). Moreover, this finding shows that the mechanism leading to the Anterior Positivity does not depend on the participants' conscious expectations, as the Anterior Positivity component arose even though participants expected the incongruent target word. Since the Anterior Positivity is not a central topic of the present study, we will not delve into these issues any deeper.

To sum up, inducing a prediction for the target word (induced-prediction congruent and induced-prediction incongruent) affected two components at the target word: it completely obliterated the N400 component thanks to preactivation of the word. It also led to the old/new positivity due to repeated presentation of the target word. Both incongruent conditions (induced-prediction incongruent and no-induced-prediction incongruent) led to a P600 component, because of greater attention attracted by the incongruity and/or engagement of repair processes. They also led to an Anterior Positivity component, presumably reflecting the need to rebuild the situation model such that it can accommodate the actually presented word. The two manipulations interacted within the N400, where inducing prediction had a precedence over incongruity (in the induced-prediction incongruent condition), directly supporting the preactivation view of the N400 and arguing against the integration view.

4.2. ERPs at the intervening words – what are the ERP correlates of holding an explicit lexical prediction while processing a sentence?

The second question we explored was how carrying a specific lexical prediction affects sentence processing, when the prediction does not directly concern the currently processed words. The ERPs at the intervening words provide us with the possibility to address this question. Let us first focus on the ERPs obtained at the words preceding the verb. For both word positions before the main verb of the story-final sentence (first word of the sentence and word directly preceding the main verb) we saw a frontal negativity for the induced-prediction conditions (induced-prediction congruent and induced-prediction incongruent), relative to the no-induced prediction conditions (no-induced-prediction congruent and no-induced-prediction incongruent). This effect suggests that the predicted word became stored in working memory, in line with previous research showing that storing verbal material in working memory is associated with sustained anterior negativities (e.g. Fiebach, Schlesewsky, & Friederici, 2001; King & Kutas, 1995; Matzke, Mai, Nager, Rüsseler, & Münte, 2002; Phillips, Kazanina, & Abada, 2005; Vos, Gunter, Kolk, & Mulder, 2001).

Importantly, the ERPs preceding the main verb in the induced prediction conditions did not differ between the congruent and the incongruent condition and remained on top of each other. Moreover, they did not differ in the N400 amplitude from the no-induced-prediction conditions. This suggests that the (induced) predicted word did not affect the difficulty of accessing the intervening words and that the predicted word was not integrated with the conceptual representation of the story at the intervening words preceding the main verb.

This situation changed at the main verb. Here, for the first time, the waveforms in the induced prediction conditions diverged, depending on whether the predicted word was congruent with the story or not (induced-prediction congruent vs. induced-prediction incongruent). When participants were induced to predict the incongruent noun (induced-prediction incongruent condition), a late N400 ensued. When prediction of a congruent word was induced (induced-prediction congruent condition), the waveforms aligned with the ERPs for the no-induced-prediction conditions (no-induced-prediction congruent and no-induced-prediction incongruent).

We propose that the modulation within the late N400 time-window reflects access to the (induced) predicted target noun which had been stored in working memory. This access was triggered by the presentation of the main verb, because its syntactic properties cued that the target noun might directly follow in the sentence: All target words were nouns and they were explicitly marked as direct objects in the prediction inducing information (i.e. they were given in the accusative). Since in Polish the most common word order is SVO, it is typical for direct objects to occur just after transitive verbs and this is what participants might implicitly expect.

This proposed mechanism shares many characteristics with the processing of filler-gap sentences. There, a filler is passively stored in working memory (accompanied by anterior negativities; see e.g. King & Kutas, 1995) until a gap is encountered. At some point in the sentence, a gap is identified based on the syntactic properties of the sentence. At the gap, the filler is reaccessed and integrated with the sentence. When the filler is incongruent with the sentence, a late N400 is elicited (Garnsey, Tanenhaus, & Chapman, 1989; see Callahan, 2008 for a review).

Similarly, in the present study, access to the predicted target noun elicited the late N400 in the induced-prediction incongruent condition, because the representations of the predicted (incongruent) target word were not activated by the preceding context. The induced-prediction congruent condition did not lead to a negativity, because the representation of the predicted (congruent) word had already been activated by the context and thus accessing the predicted target word required no cognitive effort. However, from the main verb onwards, the representation of the target word was active both in the induced-prediction congruent and induced-prediction incongruent condition. This is clearly reflected in the ERPs elicited by the target word presented after the verb. There, the induced-prediction incongruent condition did not lead to an N400. Thus, if we focus on the incongruent word only, it had to become activated at some place in the sentence (and evoke an N400). When no prediction for the incongruent word was induced (no-induced-prediction incongruent), the N400 was triggered by the presentation of the target word itself. When the prediction was induced, the N400 was shifted from the target noun to the preceding main verb. Thus, according to this explanation, the N400 not only reflects the level of prior activation of the word at hand, but it also reflects the process of activating the word. Moreover, the late N400 at the verb in the induced-prediction incongruent condition seems to be *causally* responsible for the absence of the N400 at the target noun.

Let us focus now on the question why the N400 at the main verb was delayed in comparison to the classic N400. In our study, the N400 at the main verb started at 400 ms, lasted until 600–700 ms and had no clear peak. The classic N400 occurs in the 200–500 ms time-window and clearly peaks at around 400 ms (compare the late N400 obtained in the induced-prediction incongruent condition at the verb with the classic N400 obtained in the no-induced-prediction incongruent condition at the target noun, Figure 4).[4] We propose that there is a simple explanation for the delay of the N400 at the verb. We assumed that access to the expected word will occur at the main verb because, as a transitive verb, it opens a slot for a direct object, a position that the predicted direct object noun can nicely fit in. However, the information that the word at hand is a transitive verb does not become available instantly. Rather, accessing the predicted noun at the verb is syntactically mediated (by the transitivity of the main verb) and thus takes longer than directly accessing the noun on the basis of visual (or auditory) information of the noun itself.

To sum up, the predicted word did not get immediately integrated with the context at the point of its induction. To avoid disrupting the processing of the sentence, the word was stored in working memory and kept there until it became relevant. The main verb was the point where the target word became relevant, because SVO is a typical word order for Polish and because the predicted word was clearly case-marked (accusative) as a direct object. Thus, the transitive verb opened up a structural slot into which the predicted noun could fit. This triggered the retrieval of the predicted word from working memory and the activation of its conceptual representation in long term memory. When these representations had not already been activated by the processing of the preceding context (induced-prediction incongruent condition), accessing the predicted word was accompanied by a (late) N400 component, relative to when the predicted target noun was co-activated by the preceding discourse (induced-prediction congruent condition). Due to the preactivation occurring at the verb, the subsequent presentation of the target word in the induced-prediction incongruent condition did not elicit an N400, despite its incongruity with the preceding context.

It should be kept in mind that the analyses at the intervening words are exploratory and will require independent replication. However, the similarity of the effect at the verb to findings in other predictions studies using different paradigms (Garnsey et al., 1989; Szewczyk & Schriefers, 2013; see section 4.4) shows that this result might be not accidental.

4.3. Potential caveats

We have just presented a neurocognitive account of how an induced prediction affects the processing of the story-final sentences. Before we accept this account, we need to consider three potential caveats.

The first caveat concerns our conclusion that the predicted word started to affect the processing of the story-final sentences only at the main verb, and that this effect was driven by syntactic properties of the main verb. Our interpretation stemmed from the observation that the ERPs for the induced prediction conditions diverged from each other at the main verb, but not at the preceding words. However, it could be possible that processing at all intervening words was affected by the extent to which the predicted word was congruent with the discourse representation. The reason why this was not captured by the ERPs might be that the materials were calibrated only just after the main verb and thus the distinction between congruent and incongruent target words was valid only there. For earlier word positions in the story final sentence, this distinction between congruent and incongruent target words might not be an adequate index of the congruency of the predicted target word with the story. The ERPs for the induced-prediction congruent and induced-prediction incongruent conditions could potentially diverge also at the words preceding the main verb, if a more adequate index of congruity would be used, an index that would be tailored individually to each of the tested positions in the story-final sentence.

To test this hypothesis, we ran a post-hoc study. The aim of this study was to obtain an (continuous) index of the association between the target word and the story at various points of the story-final sentence and then to use this index as a predictor of the ERP amplitudes. In a paper-and-pencil test, a group of 63 participants was given a list of all stories, truncated at the points at which the ERPs had been analysed: before the first word, before the word preceding the main verb, and before the main verb. Participants were asked to assess how likely it would be that a given word (congruent or incongruent target word) could occur somewhere in the rest of the truncated sentence. It was stressed that the word would not need to appear as the next word. The construction of this task thus mimics the knowledge of participants of the EEG study at various points of the story-final sentence. We then used the obtained plausibility indices as predictors in the analysis of ERPs. The results were very similar to the analysis using the original factor Congruity. Despite the fact that the new plausibility index was calibrated for each analysed intervening word separately, the index differentiated the ERPs for the induced-prediction congruent and induced-prediction incongruent conditions only at the main verb, but not at the preceding words. This analysis thus unambiguously shows that the divergence of the ERPs for the induced-prediction congruent and induced-prediction incongruent conditions at the main verb was caused by the (syntactic) properties of the verb. It supports our conclusion that the access to the target word at the main verb was triggered by the syntactic properties of the verb. A detailed description of this additional analysis is presented in Supplementary Materials S3.

The second caveat is that, at the position where the prediction of an incongruent word was induced, participants might instantly realise that this word is going to be incongruent and they might alter the way they processed the story-final sentence. This possibility is supported by the fact that congruent words were judged as more plausible from the onset of the story-final sentence. Thus, it is possible that participants could even "give up" on conceptual processing of the story-final sentence, once they had realised that the induced-prediction word was not going to make sense. This interpretation would also explain the absence of the N400 at the target noun in the induced-prediction incongruent condition: since participants abandoned processing the sentence, there was no N400 at the target word.

However, we do not think this alternative interpretation is correct. First, the ERPs show that until the main verb, participants processed the story-final sentence in exactly the same way when the predicted word was congruent and when it was not. Second, if participants gave up on processing the story-final sentence in the induced-prediction incongruent condition, this condition should not elicit the late N400 at the main verb. Finally, if participants processed the story-final sentences in the induced-prediction incongruent condition less deeply, in the post-experimental sentence recognition test they should recall less stories in the induced-prediction incongruent than in the no-induced-prediction incongruent condition. The results, however, show that this was not the case; participants recalled the same number of incongruent stories with and without an induced prediction. Thus, congruity of the word for which the prediction was induced did not affect the level of processing of the story-final sentences.

A final caveat concerns the possibility that the N400 component may not be an appropriate neural signature to help distinguish between the preactivation and integration theory of the N400, because the component may index multiple processes, one of which could be conceptual integration. In principle, it is possible that the N400 component reflects some aspect of conceptual integration and this idea has been even suggested within preactivation accounts (Kutas & Federmeier, 2011; Van Berkum, 2009). That is to say that it is possible that during the N400 time-window the conceptual representation of a word is activated *and* at the same time this activation affects the representation of the discourse, for example because the words' meaning is not simply retrieved but rather dynamically constructed to fit the current context (Elman, 2009; Laszlo & Federmeier, 2011). Our study shows that if a word is preactivated (and thus predicted) with sufficient strength, all these potential computations that are potentially reflected in the N400 component can be carried out before the target word.

The account just discussed should not be confused with the integration theory of the N400 that we referred to throughout this paper which assumes that lexical access and integration occur in a serial order, and that the N400 only reflects the latter process and can thus not be regarded as reflecting prediction (Hagoort, 2008; see Kutas & Federmeier, 2011 for a discussion). When we evaluated this latter account, our data clearly showed that the N400 amplitude reflects the degree of preactivation and not the ease of integration once the target word appears as a part of the sentence.

4.4. A mechanism of predictions in natural language processing – a hypothesis

In the final part of this article we propose a hypothesis concerning predictions in natural language processing. Obviously, inducing predictions as in the present study is artificial and does not necessarily reflect natural predictions. However, the late N400 effect at the verb in the induced-prediction incongruent condition provides a link to studies measuring natural predictions. This late N400 effect is very similar to N400s found in studies using a paradigm in which the prediction of a noun is measured at a preceding word (DeLong, Groppe, Urbach, & Kutas, 2012; Martin et al., 2013; Otten & Van Berkum, 2009; Szewczyk & Schriefers, 2013; Wicha et al., 2004; Wicha, Bates, Moreno, & Kutas, 2003; Wicha, Moreno, & Kutas, 2003). For example, in a previous study (Szewczyk & Schriefers, 2013) we presented short stories, similar to those used in the present study. The stories made it very likely that a target noun will be animate or inanimate. The target nouns were preceded by adjectives whose grammatical gender agreed or disagreed with the animacy of the expected target noun (this was possible because in Polish – the language used in this study – animacy co-determines grammatical gender). The ERPs for adjectives with prediction-consistent and prediction-inconsistent gender differed, indicating that a noun (and its grammatical gender) was predicted before it was presented. Until now, however, there is no clear account of the mechanism that underlies the ERP effects at the adjective in the study by Szewczyk and Schriefers (2013) and in other studies looking for evidence of noun predictions at prenominal elements.

In our previous study, the adjectives with a prediction-inconsistent gender marking led to a late N400 component. Because of the similarity of the time-course, polarity and scalp distribution between the late N400 obtained in the present and in our previous study, we can extrapolate the conclusions drawn within the present study to understand the mechanism giving rise to the prediction effect in our previous study. As a reminder, in the present study the late N400 was triggered by the identification of the syntactic properties of the verb (i.e. the verb's transitivity). This component reflected access to the target noun and thus it was directly responsible for the absence of the N400 at the target noun itself. We would like to propose that the effect obtained at the adjectives with prediction-inconsistent gender marking also reflected an attempt to access nouns that would be both semantically congruent with the preceding context and have a grammatical gender that is congruent with the gender marking of the adjective. In other words, we propose that the effect at the adjectives reflected an update of prediction, triggered by the syntactic information contained in the gender marking suffix of the adjective. Adjectives with prediction-consistent gender did not evoke a similar late N400 component, because in this case, the gender-suffix did not bring any new information: By the time the prediction-consistent adjective was processed, some nouns congruent with the gender of the adjective had already been preactivated. Thence, no prediction updating was necessary.[5]

In sum, the hypothesis that N400-like negativities at the prenominal elements reflect updating of prediction is in line with theoretical and computational models (see Introduction) showing that the amplitude of the N400 corresponds to the degree in which the representation of the discourse has to be updated on the basis of new information (Frank, Otten, Galli, & Vigliocco, 2013, 2015; Kutas & Federmeier, 2011; Rabovsky & McRae, 2014).

Accepting this hypothesis has two theoretical consequences. First, it reveals the dynamics with which predictions are made: once a bit of new information becomes available, predictions are instantaneously updated. Second, it shows that predictions can integrate information coming from many levels of the linguistic hierarchy. In the examples described above, syntactic information (identification of the grammatical category of the verb) or morphosyntactic information (the gender marking on the adjective) triggered the activation of conceptual representation of the word stored in working memory (the present study) or in long-term memory (Szewczyk & Schriefers, 2013). In this latter case, selection of the activated words was presumably under constraints that also spanned many levels of the linguistic hierarchy: syntactic (accessed words should be nouns, because adjective requires a noun to follow), morphosyntactic (the accessed words should be of a specified gender), and semantic (the preactivated words should fit the semantic context of the story). This conclusion is in line with the dual-pathway model of prediction in language comprehension by Chang, Dell, and Bock (2006; Dell & Chang, 2014), in which structural and conceptual constraints are used to predict the words that might occur next in the message. It is also in line with proposals that all layers of the language hierarchy interact in generating predictions (forward models; e.g. Pickering & Garrod, 2013). Overall, these two consequences resonate with the assumption of maximal incrementality in language comprehension (Altmann & Mirković, 2009).

Note that some studies obtained an N400 at the prediction-inconsistent prenominal word that was not late, i.e. it occurred within the standard N400 time-window (DeLong et al., 2012; Martin et al., 2013; Otten & Van Berkum, 2009; Wicha, Bates, et al., 2003; Wicha, Moreno, et al., 2003, 2004). In terms of the hypothesis we propose here, the latency of the N400 should be determined by the timing with which the relevant information triggering a prediction update becomes available. In the Szewczyk and Schriefers (2013) study and in the present study the critical information was encoded in the syntactic or morphological properties of an open class word: in the gender marking suffix of adjectives or in the transitivity of the verb. In contrast, in the studies in which the N400 at the prenominal element had a classical N400 time-course, the relevant information was encoded in closed-class words, for example the grammatical gender encoded in Spanish determiners (Wicha, Bates, et al., 2003; Wicha, Moreno, et al., 2003). In closed-class words, the information triggering a prediction-update is presumably lexicalised, which speeds up its availability, and thus explains the earlier onset of the N400 at the prediction-inconsistent prenominal word (see also Szewczyk & Schriefers, 2013 for a discussion of when gender information becomes available).

4.5. Conclusions

In this study we experimentally dissociated two factors that have been proposed as the driving forces of the N400 amplitude in sentence processing: the preactivation of a word versus the congruity of a word with the preceding context. We found that a target word that is preactivated does not elicit the N400 component, even when the word is incongruent with the context. This finding directly supports the preactivation theory of the N400, and thus supports the view according to which predictions are widespread and are a central element of language comprehension (c.f. Huettig & Mani, 2016). This suggests that most of the modulations of the N400 component can be treated as a consequence of changes in the state of brain activation taking place before the critical word has been processed (in line with the conclusions of a review of thirty years of research on the N400; Kutas & Federmeier, 2011).

We also traced how a specific lexical prediction is carried from the point of its induction to the point where the predicted word occurs in the sentence. We showed that the prediction has no impact on sentence processing, until a point where the predicted word has a syntactic fit with the unfolding sentence. At that point the predicted word is activated in long term memory, and this is reflected by a late N400 component. We showed that this activation is directly responsible for the absence of the N400 component at the target word itself. In other words, we captured the moment of the actual implementation of prediction (preactivation of the target word) and its consequences for the processing of the predicted word. This suggests that the N400 not only reflects the consequences of activating a word (i.e. the word's level of activation), but it also reflects the actual process of activating the word. Our account further entails that in natural sentence processing, predictions are instantaneously updated, whenever a new piece of information, in our case the morphosyntactic information of the verb preceding the critical (preactivated) word, becomes available.

Notes

1. Note that the version of prediction as preactivation is not necessarily the same as postulated by the predictive coding theory where prediction is seen as the facilitated processing of a stimulus at the neural level (see Lewis, Schoffelen, Schriefers, & Bastiaansen, 2016; see also Kuperberg & Jaeger, 2016 for an in-depth discussion of different levels of prediction).
2. The broad range of cloze probability values is due to the fact that the target words occur in stories with a broad range of constraint strength values. Within each context, the congruent target word is one of the most

likely words, and thus is highly plausible with respect to its context. In Supplementary Materials (S2) we capitalise on the large variance of constraint strength values to test how constraint strength affects the magnitude of the Anterior Positivity effect.
3. A parallel analysis performed using baselines directly preceding the point of divergence between the induced-prediction and no-induced-prediction conditions yielded a similar, although noisier and less reliable pattern of results.
4. Even though some differences in the latency of the N400 have been reported (see e.g. Brothers et al., 2015), they are far smaller than the discrepancy obtained here.
5. The idea that the effects at prenominal words reflect an update of conceptual predictions has been independently proposed by Nieuwland et al. (2017). In an experiment designed specifically to test this hypothesis we have just obtained results fully supporting it. The results show that the effect at a prenominal word has causal consequences for the N400 on the following noun and its amplitude is graded, depending on the amount of prediction updating triggered. Moreover, the amplitude on the noun itself is also graded depending on the amount of prediction updating triggered by the preceding word (Szewczyk, 2017).

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Appendix A

Below are examples of four items, differing in the number of intervening display frames (see section 2.2) and in cloze probability of the congruent target noun. The critical story-final sentences are given in Polish (P), in literal English translation (LE), and in English translation (E). The critical direct object nouns are given in bold, in the following order: congruent noun (indicated by (c)), incongruent noun (indicated by (ic)).

Item #1 (9 intervening display frames, CP = 0.83, constraint strength = 0.83)

My uncle loves to make practical jokes. During the last summer he mounted a triangle fin on his back, jumped into the water and approached the swimming area with his fin only above the water.

P: Narobił się straszny raban i wszyscy byli przekonani że ujrzeli **rekina (c) / lekarza (ic)** podpływającego do nich.

LE: There-started-to-be terrible fuss and everybody were convinced that they-saw **shark (c) / doctor (ic)** swimming up-to them.

E: There was terrible fuss and everybody thought they saw **a shark (c) / a doctor (ic)** approaching them.

Item #2 (7 intervening display frames, CP = 0.37, constraint strength = 0.37)

Children played soccer in a yard next to an old tenement. Suddenly one of the boys kicked the ball so unfortunately that it broke a window of one of the apartments on the first floor.

P: Skruszony malec zapukał do drzwi mieszkania i przeprosił **właściciela (c) / mistrza (ic)** ze spuszczoną głową.

LE: Repentant kid knocked on door of-apartment and apologised-to **owner (c) / master (ic)** with lowered head.

E: The repentant kid knocked on the door of the apartment and apologised to **the owner (c) / a master (ic)** lowering his head.

Item #3 (4 intervening display frames, CP = 0.95, constraint strength = 0.95)

Jonas promised his fiancée to make a bookshelf for her. After he prepared planks and nails, he realised that he did not have anything that he could use to attach the bookshelf to the wall.

P: Dopiero gdy od sąsiada pożyczył **młotek (c) / walkę (ic)** z werwą zabrał się za pracę.

LE: Only when from neighbor he-borrowed **hammer (c) / fight (ic)** with vigour he-started working.

E: Only when he borrowed **a hammer (c) /a fight (ic)** from his neighbor he started to work vigorously.

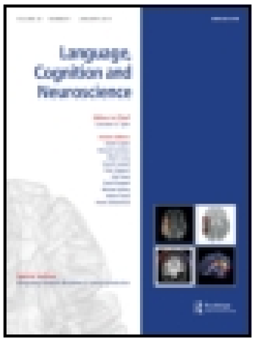
Item #4 (3 intervening display frames, CP = 0.21, constraint strength = 0.37)

A circus was preparing a new performance. Together with their trainers all animals were practicing new acts. Suddenly, one of them tripped, dropping a ball from its trunk.

P: Treser natychmiast skrzyczał **słonia (c) / ochroniarza (ic)** zestresowanego nową sytuacją.

LE: The trainer immediately scolded **elephant (c) / bodyguard (ic)** stressed by-new situation.

E: Immediately, the trainer scolded **the elephant (c) / a bodyguard (ic)** who had been stressed by the new situation.



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The N400 as an index of lexical preactivation and its implications for prediction in language comprehension

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